ROGER L. BATTEN

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SYMPOSIUM ON FIFTY YEARS OF PALEONTOLOGY

ADEQUACY OF THE FOSSIL RECORD

NORMAN D. NEWELL
American Museum of Natural History and Columbia University, New York, New York

ABSTRACT—During the history of the Paleontological Society there have been many important developments in paleontology. In addition to steady increase in knowledge through new fossil discoveries, increasing attention is being given to ecological and evolutionary processes, and there is growing concern with theory and principles in both the biological and geological aspects of paleontology. There is, however, a neglect of comparative morphology and taxonomy, and there are far too few expert paleontologists to cover the work to be done.

For a qualified few who recognize the challenge, opportunities are almost unlimited in paleontology for significant studies of comparative morphology, systematics, evolution, stratigraphic facies, paleoclimatology, and the general history of life. The utilitarian value of fossils as stratigraphic indicators is, and will always be, an important aspect of paleontology. But, as requirements become ever more exacting, stratigraphic paleontology calls for skilled preparation of fossils and expert knowledge of their biological nature beyond the abilities of the non-specialist.

Intensive stratigraphic studies in all parts of the world, and the development of improved methods of collecting and preparing fossils have revealed a fossil record much richer than was envisioned by the founders of the Paleontological Society. There are now substantial reasons for believing that the available record is still very incompletely known. Much remains to be learned about the processes by which organisms are preserved as fossils.

INTRODUCTION

IT IS a pleasant custom to celebrate the anniversaries of outstanding events and it is appropriate and useful at such times to take note of progress and trends in human affairs. This year, 1958, is the Jubilee anniversary of the founding of the Paleontological Society. It is also the centennial of the first public announcement by Darwin and Wallace of their theory of evolution by natural selection; and it is the bicentennial of the publication of the tenth edition of Linnaeus' *Systema Naturae* from which stems our method of naming animals and plants. This year is also notable as a year of compromise and agreement among paleontologists and neontologists with respect to revisions of the international code of zoological nomenclature. These were all events of great importance in the history of paleontology.

BIRTH OF THE PALEONTOLOGICAL SOCIETY

Fifty years ago, in Baltimore, at a meeting of the Geological Society of America, thirty-four paleontologists convened under the chairmanship of Charles Schuchert to create a new organization of paleontologists out of the existing Society of American Vertebrate Paleontologists. The plan was to broaden the scope of that group to include students of fossil invertebrates and plants. If was thought that it might be mutually rewarding for paleontologists of varied interests to meet together at least once a year to exchange views about the problems of common interest. Thus was born the Paleontological Society, the stated purpose of which was the "promotion of the science of paleontology." The charter members, including many of the greatest figures of American paleontology, wise in the knowledge of their time, were Ami, Arnold, Bagg, Bassler, Beede, Berry, Case, W. B. Clark, J. M. Clarke, Cook, Cumings, Foerste, Gidley, Gilmore, Grabau, Kirk, Knowlton, Loomis, Lull, Matthew, Osborn, Prosser, Raymond, Riggs, Savage, Schuchert, Shimer, Stanton, Ulrich, Walcott, Weller, White, Williams, and Williston.

The program[1] of the first annual meeting of the Society reflected great interest in

[1] Papers by Clarke, Calvin, Bassler, Sinclair, Schuchert, and Knowlton were published in Popular Science Monthly, vol. 76, p. 581–603, 1910. See also, Cleland, 1910.

fundamental problems of paleontology. Two of the papers were devoted specifically to the adequacy of the fossil record and these have suggested the title of my remarks.

In 1908, as now, the study of fossils had many different facets: stratigraphic, morphologic, taxonomic, geographic, ecologic, evolutionary, and so on. For some persons, especially the students of fossil plants and vertebrates, paleontology was an exciting quest providing records of organic evolution, and climates and ways of life long past. For others, mainly invertebrate paleontologists occupied with the practical business of making geologic maps and classifying and correlating strata, paleontology was a kind of philately in which the fossils were the postage stamps and the postmark of their organic origin was ignored. From the very beginnings of our science there have been two schools, those who study fossils in order to understand stratigraphy, and those who study fossils in order to learn about past life. It is unfortunate that these two points of view are sometimes regarded as mutually incompatible because they need not be. They should supplement each other in building a well-balanced science of paleontology. Surely, neither group has a monopoly in the knowledge of fossils and both approaches to paleontology can be rewarding.

In the early days, varied approaches to paleontological problems were judged to be highly beneficial for the science and all aspects of paleontology were well-represented in the Society. In recent years, however, specialization and increasing divergence of objectives have wrought sweeping changes in the Society. The paleobotanists, always few in numbers, now are allied with the Botanical Society. The vertebrate paleontologists have their own society. Many individuals in both groups retain membership in the Paleontological Society. In this way their needs are best served. The activities of a great majority of the members of the Paleontological Society now lean strongly toward the stratigraphic aspects of invertebrate paleontology, physical stratigraphy, and sedimentation.

In a presidential address to the Paleontological Society, G. Arthur Cooper (1958) has given a comprehensive and able summary of recent developments in paleontology. I lend my whole-hearted support to his plea for more paleontology of higher quality. The fossil record is much richer than we formerly supposed and we need to give much more attention to discovery and description of fossils for the purposes of both geological and biological paleontology. This is fundamental.

The opportunities in paleontology are greater and more rewarding than ever before. There is a steady demand by universities, museums, and geological surveys, and petroleum companies for young men who are broadly trained in paleontology and equally expert in studies of fossils and sedimentary rocks. There are many competent stratigraphers but too few of these really understand fossils, and the demand for able paleontologists greatly exceeds the supply. Why is this true?

No doubt this is a reflection of a traditional antipathy of physical scientists for the disorderly nature of biology, an attitude shared, unfortunately, by many stratigraphers with strong preferences for the physical aspects of historical geology. Some of these are charged with teaching paleontology to impressionable university students and thereby transmit and perpetuate their prejudices. In view of the vast contribution to human knowledge that paleontology has made, and continues to make, it is astonishing that this subject receives less recognition among many earth scientists than, say, oceanography, or seismology. Biological geology receives less than enthusiastic endorsement from a majority of physical geologists.

In the physical sciences, particular conditions tend to produce predictable results, within the limits of observational error. For example, the laws of physics and chemistry can be mathematically expressed and their operation can be tested as often as desired. The passage of time does not affect the results. Gravity does not have a history. This appeals to those who feel that nature is inherently systematic and orderly.

In contrast, the situation is infinitely more complex and difficult in the biological sciences because each organism in many ways is unique. Broadly speaking, evolution is irreversible. History does not repeat itself, and a particular type of organism is never

again exactly reproduced after becoming extinct or extensively modified. Every flora and fauna is unlike every other one. The fossil record consists of a succession of evolving forms which vary not only through time but also along each stratigraphic horizon. Many scientists are uncomfortable in the face of such proof of the inherent complexity of organic nature.

Thus, the fossil record and the evolutionary sequences that it illustrates are complex, immeasurably more complex and more difficult of analysis than the record of the rocks. The study of fossils cannot be mechanized through application of labor saving instruments, and it is indeed doubtful that it will ever be possible to study fossils on a truly mass production basis.

Probably these are some of the reasons why stratigraphers now outnumber paleontologists five or six to one in the Palentological Society.

In spite of a chronic shortage of paleontologists, however, there have been remarkable advances in knowledge about fossils in the past fifty years. These include not only the gradual accumulation of new facts through continuous collecting, but they also include revolutionary changes in our methods and attitudes toward fossils. Indications of these changes are found in the mounting flood of great philosophical works, textbooks, and handbooks on fossils that are appearing with increasing frequency. Among these, the *Treatise on Marine Ecology and Paleoecology* and the *Treatise on Invertebrate Paleontology*, both conceived by the membership of this Society, provide impressive testimony of exciting new developments. They clearly show that paleontology is today broader and more vigorous than it was fifty years ago, even though the ratio between productive paleontologists and physical geologists unquestionably has dropped.

Stratigraphic paleontology enjoyed an impetus after the sudden growth of commercial micropaleontology in the early 20's. But the truly revolutionary developments of the past three decades are 1) improvements in techniques of collecting, preparing and describing fossils, 2) recognition of the special importance of populations in taxonomy and evolution, 3) increased attention to the ecological aspects of fossil communities as the key to the meaning of stratigraphic facies, 4) the application of statistical methods in the analyses of all sorts of paleontological problems, and 5) the geochemical studies of fossils. These subjects will, doubtless, be treated in the papers that follow.

Comment is in order here on the recent application of electronic IBM computers in the solution of paleontologic problems. This is, I believe, more than just another statistical technique. Studies of animal morphology by Olson and Miller, and biofacies analysis by John Imbrie, involve statistical analyses of scores of variables. Problems of excessive complexity now can be attacked quickly and efficiently. In the near future, we may have at our disposal the means for more or less routine quantitative solutions of all sorts of paleontological problems involving complex interrelationships of many variables.

WHAT IS THE FOSSIL RECORD?

An important gain in paleontology during the past fifty years has been a gradual increase in appreciation of the positive merits of the fossil record. A century ago, Charles Darwin was preoccupied with the deficiencies in the record, and his two "geological" chapters in the *Origin of Species* reveal a remarkable insight into the problems of stratigraphic paleontology.

In reality, there are two aspects of the fossil record, and it is worth-while to distinguish clearly between them. One is the published, more or less adequately known, record. The other is the undiscovered, but potentially knowable, record. In discussing the nature of the fossil record, few writers have clearly distinguished between the two.

The known record may be regarded as a sample from which we periodically draw inferences, not only about past life but also about the potentially knowable fossil record. The known record increases gradually and our interpretations evolve with new discoveries, but the potentialities of the record do not change. In the remarks that follow, "fossil record" will be understood as the total record unless otherwise qualified.

THE TEST OF RELIABILITY

Fifty years ago, some of the participants in the first scientific sessions of our Society

took a much more optimistic view of the merits of the fossil record than did Darwin. Nevertheless, there is still a lively debate going on with respect to the validity of many general conclusions and inferences from fossils about past life. Doubtless, it may be a long time before we are prepared to make a final evaluation about the adequacy of the record for certain general conclusions. There is general agreement, however, that many striking patterns of fossil distributions have been confirmed independently hundreds of times. Reproducibility of general conclusions in paleontology, as in other sciences, is the best test of reliability. The abrupt appearance of the Cambrian fauna; the rise and decline of the ammonoids, primitive mammals, and trilobites; the explosive spread of the angiosperms; the world migrations of land mammals during the Tertiary; and mass extinctions near the close of Permian, Cretaceous, and Pleistocene times—these and hundreds of other generalizations about the fossil record—are based on a great body of observational evidence. They have been accepted for so long that we regard them as established truths of geologic history.

Not all well-documented paleontological evidence permits unequivocal conclusions, however. For example, modern studies of paleomagnetism in sedimentary rocks have suggested to some investigators great migrations of the magnetic, and possibly the geographic, poles throughout geologic time. Extensive studies of relative growth rates of fossil corals have led Ting Ying Ma likewise to the conclusion that the earth's poles have migrated (Ting Ying Ma, 1957, and earlier papers).

On the other hand, the distribution of land plants after the middle Paleozoic indicates latitudinal zonation in climatic belts approximately parallel to the present equator (Chaney, 1940; Edwards, 1955). Latitudinal zonation is also well-marked among many groups of marine invertebrates; for example, the Cretaceous rudistids and whole faunas of the Permian and Tertiary periods (Stehli, 1957; Durham, 1958).

Well-documented knowledge about distribution of fossils in time and space is cumulative. The extension of known ranges by means of new discoveries does not upset or invalidate earlier conclusions, as is sometimes claimed, but simply requires modification of prior conclusions based on less complete data. For example, the unexpected discovery of living coelacanths and monoplacophorans, supposed to be long extinct, does not affect interpretations of the early history of these animals.

RICHNESS OF THE FOSSIL RECORD

It has long been accepted that the fossil record is not a random sample of past life. For the most part, the record consists mainly of skeletal parts of organisms that lived within, or near, sedimentary basins. Even among these organisms there is only a very poor fossil representation of soft-bodied forms. The organisms of upland areas and deserts are rarely found preserved as fossils. It is often stressed that, on the average, the chances of preservation of individual organisms as fossils are very small, indeed. But it should be kept in mind that the total number of individuals that ever lived, of even the most limited species, is always very great. In spite of low probabilities of preservation, fossils are really not uncommon. It is well-known that the individuals of many fossil species are fantastically abundant in the rocks. Even those fossils considered to be very rare must be represented by thousands or millions of individuals yet to be discovered.

During the past few years we have been compelled to revise our ideas about the overall richness of the fossil record. J. T. Gregory (1955) has shown recently that the numbers of known kinds of fossil vertebrates tend to be roughly proportional to the numbers of collecting sites. While this is certainly not so often true of fossil plants and invertebrates, there can be no doubt that we have hardly yet a good idea of the ultimate richness of the record. Strata considered to be only sparsely fossiliferous, as judged from superficial inspection, actually may contain an abundance of fossils. The degree to which this is true is shown clearly by methods of mass collecting fossils, wherein a volume of sediment or rock is dug by hand, shovel, or power machinery, washed, and sieved for fossils. This method has long been used for microscopic fossils such as spores and Foraminifera, but it also is used effectively now

for collecting larger invertebrates and bones and teeth of small vertebrates. The number of fossils thus obtained usually is greater per unit volume than the number that accumulates over a unit area of rock, and fossils collected in matrix commonly are of better quality than those that have been long exposed to the weather.

Small fossils are incredibly numerous in many strata where they are major components of the rocks. Leidy once estimated a quarter of a million Foraminifera in an ounce of marine sediment. A cubic inch of diatomaceous earth contains as many as fifteen million diatoms per cubic inch and there are many cubic miles of nearly pure diatomite along the Pacific Coast of the United States, alone. Robert Broom, the South African paleontologist, estimated that there are eight hundred thousand million skeletons of vertebrate animals in the Karroo formation. While such estimates, of course, are not highly accurate, they stress the vast difference between the known paleontological sample and the astronomic numbers of fossils remaining in the rocks.

THE NUMBERS OF FOSSIL SPECIES

Many persons have attempted to estimate the total number of fossil species recorded in the literature. Nearly fifty years ago, Schuchert (1910) estimated that there were one hundred thousand fossil species known. A recent tabulation by Muller and Campbell (1954) does not increase the earlier estimate. They find that ninety-two thousand species of fossil animals are known, and I suppose that the record of fossil plants would bring the total to around one hundred thousand.

Teichert (1956) has tried to calculate the total number of "readily preservable" animals and plants that ever lived. He has taken as a premise the view that calcareous, siliceous, or woody skeletons make up most of the fossil record and he omits consideration of soft-bodied organisms and insects, as quantitatively unimportant in the fossil record. In this, I think that he errs because very many of these are known as fossils and, surely, many more will be discovered. Although they probably are not so abundant as individuals, they may eventually exceed other kinds of fossils in variety.

According to Teichert, the numbers of species now living that would be most susceptible to preservation as fossils are:

Invertebrates	170,000
Vertebrates	49,000
Vascular plants	350,000
Total "Preservable species"	569,000

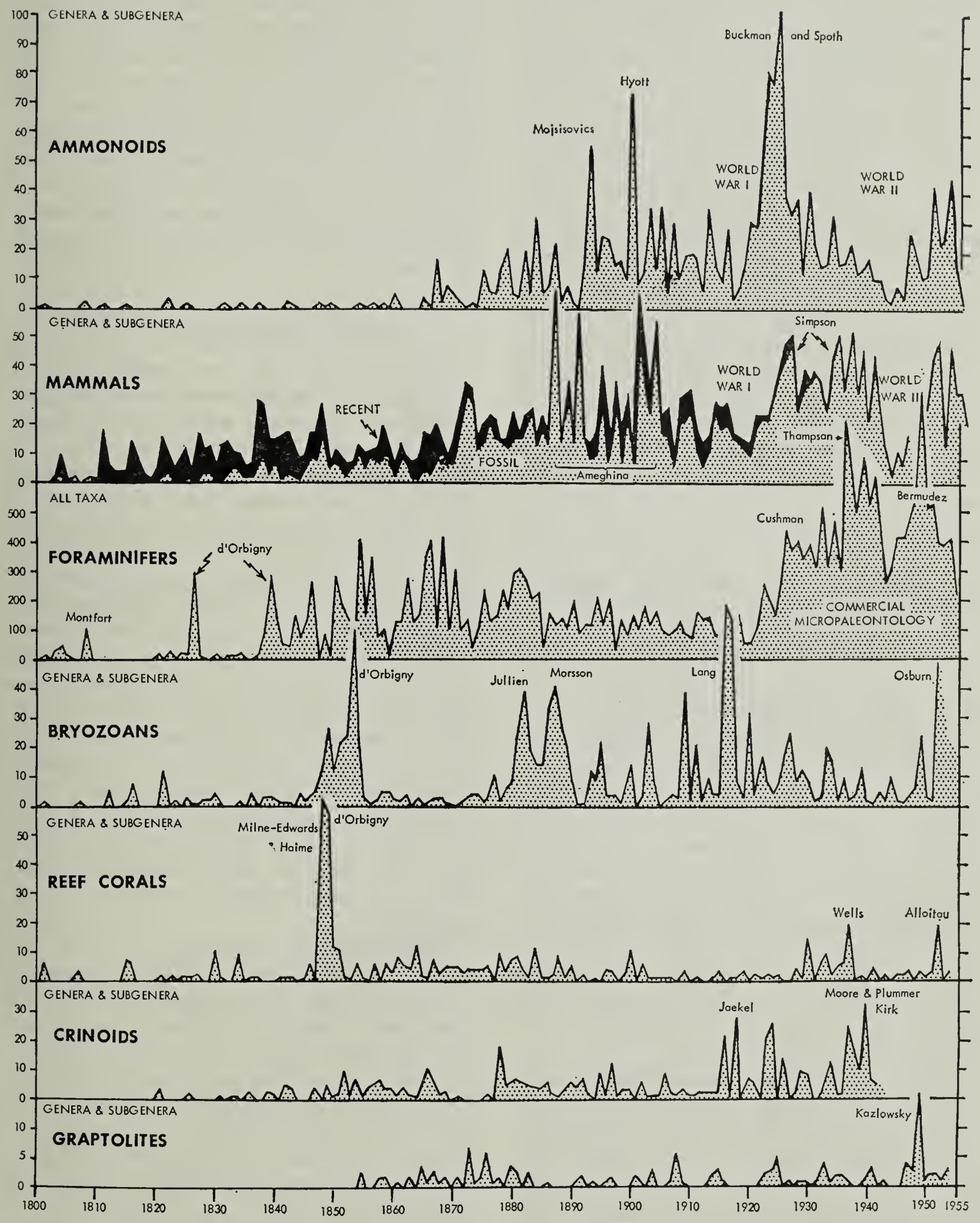
Taking twelve million years as the average length of a geological epoch, therefore the top limit for average longevity of fossil species, he concludes that the number of species of animals and plants preserved in the rocks may reach a total of ten million. I think that the estimate may be too small.

These speculations are useful in stressing the fact that the fossil record is, indeed, poorly known, and they indicate something of the magnitude of the task and opportunities ahead for paleontologists. The known record may represent not more than one percent of the potentially knowable record if Teichert's figures are of the right order. Yet, the known record reveals much of value about past life and serves as the basis for a very respectable stratigraphic system. In any case, it seems absurd to conclude that the heyday of taxonomic paleontology is over. Our problem is not similar to that of mineralogy in which the total number of species probably never will exceed three or four thousand.

RATES OF DISCOVERY OF NEW FOSSILS

A few fossil groups are becoming comparatively well-known and their taxonomy has become stabilized. This is true, for example, of the ammonites, the graptolites, and the hexacorals (Scleractinia), all of which are favored by field geologists and have been studied for a long time by specialists. New discoveries in these groups have little tendency to upset views about general phylogeny. Is there any indication that these or others are so well-known that most of the preserved kinds have already been discovered?

Publication rates provide a rough measure of discovery rates of new categories (Fig. 1). A long-sustained, or increasing publication rate of new taxa, for example, may be an indication that the supply of new



TEXT-FIG. *1*—Fluctuating publication rates in several important groups of fossils. Data from *Treatise on Invertebrate Paleontology*, G. G. Simpson, R. C. Moore, Angelina Messina, and others.

fossils is not near depletion. Minor fluctuations in publication rates are caused by the sporadic publication of monographs and by the different taxonomic philosophies of authors; and larger fluctuations are caused by war, depression, and other human vicissitudes. Long-term trends in publication are certainly significant in terms of the development of knowledge about fossil groups.

Figure 1 indicates that discovery rates in Foraminifera and fossil mammals are accelerating as the search is intensified. Excepting insects, there is no group of organisms under such extensive study as are the Foraminifera and now they may be the best known of any fossil group. According to Miss Angelina Messina (personal communication), twenty-four thousand four hundred and fifty-four species and varieties and one thousand five hundred and twenty-two genera and subgenera are listed in the Catalogue of Foraminifera through the year 1957. In contrast, the rate of publication of new genera of recent mammals gradually has dropped nearly to zero. It may be confidently inferred that nearly all of the living mammals have been discovered (Fig. 1).

The record of the ammonoids is not as clear. There is a suggestion that the rate of discovery of new ammonoids actually is declining, but it is too early to be sure of this. The recent passing of both Spath and Arkell, our leading experts in this group, certainly will cause a marked slump in ammonite studies during the next few years. The other groups of figure 1 show very low and erratic discovery rates that probably are a reflection of the fact that very few persons have worked on these groups. Surely, there is no indication in any of these data that the supply of basically new fossils is about exhausted.

The Scleractinia, or reef corals, are well-constructed for preservation as fossils, and they have been covered in comprehensive summaries by Vaughan, Wells, and others. They may be regarded as a group in which the fossil record is exceptionally well-known. Throughout the West Indian region there are innumerable elevated fossil reefs dating from Pleistocene interglacial stages. These contain a well-preserved coral fauna essentially like that still living in the region. According to Wells (1956), the Pleistocene ice ages did not cause significant extinction among the corals. On the other hand, one-third of the living hermatypic coral genera of the West Indies are not yet known in the Pleistocene rocks of the region (John W. Wells, personal communication), and the Pleistocene faunas are, at least, as well-known as are those of the Tertiary. Undoubtedly, further and more intensive collecting in the Pleistocene reefs gradually will bring to light most of the recent genera and species.

PROBABILITIES OF DISCOVERY

Influenced by the low probabilities of preservation of organisms as fossils, we have a tendency to regard well-preserved fossils as rare objects. This attitude is sure to be strengthened by hasty search or unskilled laboratory preparation. Rocks that actually are replete with well-preserved fossils are often reported as barren, or sparsely fossiliferous because the fossils do not lie in conspicuous view over the surface, conveniently freed by weathering from the rock matrix.

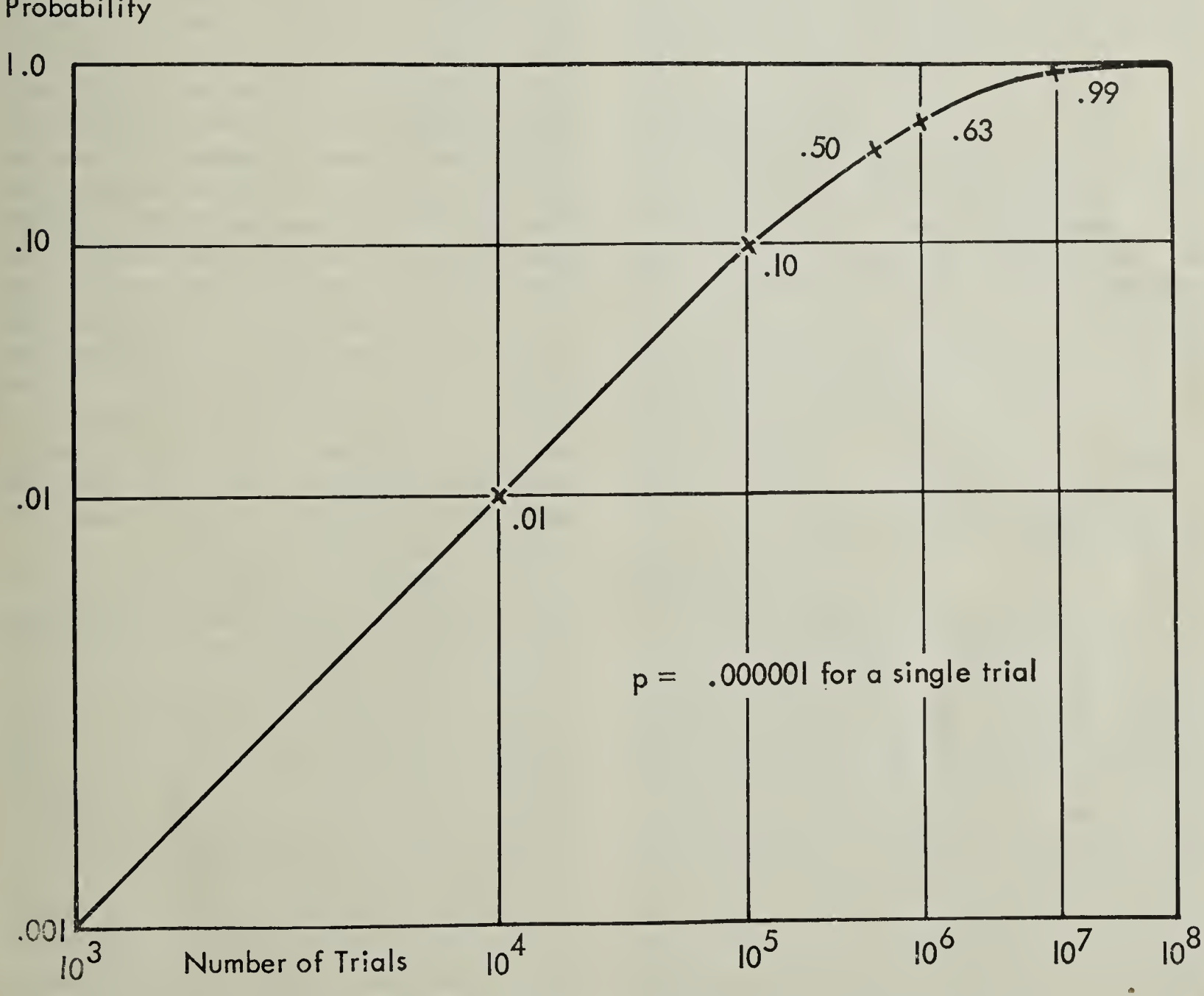
The discovery of fossils is strongly influenced by laws of chance. Consequently, patience and repeated visits to the field usually are rewarded. The preservation of fossils likewise is dependent on the chance coincidence of many factors. There is a fundamental mathematical rule that however improbable an event may be in a single trial that event becomes increasingly probable, or even inevitable, as the trials are multiplied.

The minimum probability that we are concerned with here is that a fortunate combination of circumstances may occur at least once. Among the billions of individual organisms that have made up each species, at least one may be preserved and finally discovered by an appreciative paleontologist. A probability of one to one million for an event to take place in a single trial is clearly highly improbable. If, for the sake of argument, we assume that the chances of preservation of a single organism are of this or any other order of magnitude, the probability may be increased simply by multiplying the number of organisms.

The time element, as well as number of organisms, clearly has a very important

bearing on the chances that a particular species may leave a fossil record. Let us imagine a standing population of thousands or millions of animals that breed only once a year. With an assumed probability of preservation of a really good sample of one in one million (p=.000001) in the first year, the probability of preservation increases to 0.5 in seven hundred thousand years and 0.99 in ten million years (Fig. 2). Thus, a good sample of the species has an excellent chance of becoming part of the record before the species has become extinct. The assumed probability of one in a million is much too low for the very many fossil species that are actually represented abundantly at many localities and horizons and it is too high for species that were not preserved at all.

There are innumerable well-documented records of preservation of tissues of animals and plants in pre-Quaternary rocks (Ladd, 1957). The chitinoid skeletons of eurypterids, graptolites, and chitinozoa, but little changed from the original condition, are not rare in rocks as old as Ordovician. Fossil logs of *Araucaria* with cellular structure and saprophytic fungi perfectly preserved and virtually unmodified by mineralization are abundant in the lower Cretaceous rocks of New Jersey. These were all formerly considered to be extremely rare examples of good preservation of organic substances in fossils, but they are now regarded as fairly common. Obviously, as the search for the potentially available but still unknown record is intensified, the probabilities of discovery greatly increase. Fossils which at first are regarded as rare may accumulate in collections and eventually come to be regarded as common or abundant.



TEXT-FIG. 2—Effects of repeated trials on probability where probability that an event will take place in one trial is one in a million.

QUALITY OF THE FOSSIL RECORD

During the past fifty years, we have steadily become more and more optimistic about the quality, as well as the quantity, of the fossil record. Granted that the processes of preservation are highly selective, there are, nevertheless, innumerable reports of examples of highly improbable preservation. Many of these were unknown fifty years ago. Now they are taken for granted.

Plant tissues decompose very slowly in fine-grained anaerobic bottom-sediments. Unless they are subjected to high temperatures or great pressures they may be preserved almost indefinitely with very little modification, as shown by the New Jersey Cretaceous logs. Animal tissues decompose much more rapidly than plants, but under favorable conditions they may endure for centuries with but little change. For example, large numbers of pre-Christian human cadavers are found in the peat deposits of Denmark and Holland. They are remarkable for excellent preservation of external form and fine details of tissues and organs. Little is known of the physico-chemical environment responsible for this preservation, but experimental work by Franz Hecht at the Senckenberg-am-Meer Institut near Wilhelmshaven (Hecht, 1933) shows in a general way some of the changes that may take place in animal tissues buried in water-soaked sediments. A small shark, buried for two years in water-soaked, anaerobic mud of a tidal flat, was generally well-preserved. The skin and muscles were still firm. After seven years, patches of the skin were recognizable but the carcass had deteriorated badly. Since the surrounding water-soaked sediment was soft and yielding, the body form was mainly destroyed. From his studies, Hecht learned that the protein substances decomposed very rapidly (probably liberating ammonia with resulting elevation of the pH), but the fatty substances decomposed very slowly, gradually passing into the sediment and sealing the organic mass, concretion-like, from surrounding ground waters and oxygen. Under certain conditions, the environment was acid and the shells of associated molluscs were dissolved. In other cases, where sulfate-reducing bacteria were active, the interstitial water became alkaline because of replacement of the strongly acid sulfate by sulfide, and calcareous shells were perfectly preserved. Weeks (1953) has suggested that calcareous concretions that surround fossils may have been formed by precipitation of calcium carbonate in an alkaline environment provided by ammonia from decaying protein substances. This work on fossilization is so suggestive that further studies along these lines might be fruitful.

One of the most remarkable examples of preservation of organic tissues in antiseptic swamp waters is a "fossil graveyard" in Eocene lignite deposits of the Geiseltal in central Germany, made known by Johannes Weigelt and his associates, of Halle University (Weigelt, 1935). Many animals, including groups rarely found as fossils, lower primates, snakes and birds were trapped in several small, scattered bogs where they accumulated and were preserved in anaerobic waters. More than six thousand remains of vertebrate animals and a great number of insects, molluscs, and plants were found in these deposits. The compressed remains of soft tissues of many of these animals showed details of cellular structure and some of the specimens had undergone but little chemical modification. Among the frogs were specimens in which the bones were leached away while the brain and spinal cord were preserved as adipocere Muscle tissue, connective tissue showing microscopic details, and cartilage were found in fishes, frogs, salamanders, lizards, and mammals. Small details of fly larvae and beetles, including muscle tissue, and tracheae were preserved.

Several fossils contained remains of fat cells and pigment cells containing animal pigment. Well-preserved bits of hair, feathers, and scales probably are among the oldest known examples of essentially unmodified preservation of these structures. The stomach contents of beetles, amphibia, fishes, birds, and mammals provided direct evidence about eating habits. Bacteria of two kinds were found in the excrement of crocodiles and another was found on the trachea of a beetle. Fungi were identified on leaves, and the original plant pigments, chlorophyll and coproporphyrin, were found preserved in some of the leaves. From such

ample fossil evidence, Weigelt (*op. cit.*) has reconstructed the Eocene life of the Geisel Valley in considerable detail.

There are innumerable accounts in the literature of fossil bacteria, some of which are of dubious validity. Many, however, are well-documented and are accepted by Zobell (1957). Suggestive associations of fossil bones showing evidence of disease and supposed fossil bacteria formed the basis of a classical monograph on paleopathology by Moodie (1923).

Destruction of organic remains is retarded in impervious rocks which exclude oxygen and prevent the circulation of ground water. Mollusc shells of Cretaceous age are abundant in the Coon Creek clay of Tennessee. The mother-of-pearl shells and even chitinoid ligaments of clam shells are extraordinarily well-preserved for such an old fauna. Caster and Waering (1951) discovered many remarkable articulated skeletons of the eurypterid *Megalograptus* in a clay deposit of Ordovician age. The original chitin is but little altered in these fossils and still retains a scorpionid color pattern. Chitin usually is quickly destroyed by bacterial decomposition under aerobic conditions. The preservation of these eurypterids illustrates the influence of fine-grained matrix on preservation of fossils. The horny substance of graptolites and certain protozoans is also sometimes preserved in fine-grained calcareous rocks.

The most effective preservative of fossils is fine-grained silica which may hermetically seal and protect organic remains from bacteria and ground water for hundreds of millions of years. Probably the most important development in collecting fossil invertebrates in recent years has been the adoption of mass collecting techniques that insure recovery of silicified faunas preserved in delicate detail. Almost nothing is known about the causes of selectivity in silicification of fossils (see Hellmers, 1949), but it appears that there may be two principal modes of silicification. These are not necessarily mutually exclusive and they may simply be successive stages in a single process. In the first case, organic tissues may be impregnated by opaline or cryptocrystalline silica before bacterial decomposition has destroyed essential textures and structures. The process is not yet understood, but it seems to be essentially a kind of embalming of the organic compounds in an impervious matrix of silica. Renault (1901) had circumstantial evidence that the precipitation of silica might be aided by the activities of decay bacteria. Siliceous impregnation evidently proceeds with great rapidity in some cases since remarkably delicate tissues of micro-organisms are often preserved by this means. In the second type of silicification, the original skeletal material is substituted by crystalline quartz; microscopic textures of the original material are not preserved, and the fossil is a pseudomorph of the skeleton. Examples of the two types of preservation will be considered separately.

Remarkable examples of impregnation by silica are filaments and spores of low algae and fungi found in chert of the mid-Huronian Gunflint formation of Ontario, now under study by Barghoorn and Tyler. The oldest known fossils still preserve traces of amino acids after seventeen hundred million years (Barghoorn, 1957; and personal communication).

Until recently, the oldest known land flora was a silicified lower Devonian peat bog found near Rhynie in the Scottish county of Aberdeen. Many species of beautifully preserved primitive vascular plants have been described from this locality together with the remains of many spiders, a mite, and a primitive wingless insect, all impregnated with silica. Silica impregnation is a fairly common mode of preservation of fossil plants, another outstanding example of which are the remarkable Jurassic and Cretaceous Cycadeoids, described by Wieland (1906, 1916).

Perfectly preserved chitinoid tests of early Paleozoic protozoans (Chitinozoa) and graptolites are frequently encountered in chert nodules. A great advance was made when Kozlowski discovered that many of these corneous microscopic fossils could be extracted from the hard matrix by means of hydrofluoric acid which dissolved the silica but did not affect the organic substance of the fossils. Soft-bodied microscopic organisms, including protoplasmic euglenoid protozoans, complete with flagella, have been described in Cretaceous chert in several well-documented reports by Wetzel (1953).

One of the most important discoveries of fossils preserved by siliceous impregnation are extraordinarily well-preserved uncrushed insects and other small arthropods with body hairs, appendages, and some of the internal organs preserved, found in petroliferous, calcareous nodules of Miocene age in the Calico Mountains of California. Allison Palmer (1957) found that many of the insects had been impregnated or coated with a film of silica so that they can be extracted from the calcareous matrix by means of acetic or formic acid with exquisite details intact. This discovery offers a promise that a systematic examination and chemical preparation of calcareous nodules in other formations may lead to a greatly extended knowledge of the history of insects.

Dr. W. D. Pierce, of the Los Angeles County Museum, aided by Mrs. Ruth A. Kirkby, has been systematically collecting and preparing the fossiliferous nodules. Dr. Pierce reports (personal communication) that fifty per cent of the nodules processed have yielded eggs, larvae or adult insects of many orders, with an average of 3.5 insects per nodule. One nodule contained remains of fifty insects.! In addition, there are well-preserved ostracodes, scorpionids, centipedes, mites, fairy shrimp, fish, impressions of feathers, mammal hairs, moss, algae and leaves of higher plants. Twenty-six silicified fish eggs have been found containing various stages of the embryos.

Phosphatic coprolites sometimes contain well-preserved micro-organisms that have been impregnated with silica. For example, Wilmot Bradley (1946) has described well-preserved micro-organisms of several kinds in fossil coprolites of Eocene age from Wyoming. Fossil feces belonging to reptiles and mammals contained a profusion of intestinal saprophytes closely similar to those of living forms. In addition, one of the mammalian coprolites contained large numbers of fresh water algae. The bacteria and algae were impregnated with silica and show microscopic details of structure.

These and innumerable other examples of fossils impregnated with amorphous or microcrystalline silica demonstrate the superiority of this mode of preservation and they suggest that small fossils preserved in this way are common in the fossil record.

It has been known for a long time that certain fossils may be extracted from hard rock matrix without damage by means of acids which either dissolve the matrix without affecting the fossils or dissolve the fossils without affecting the matrix. In the latter case, the resulting cavity may be used as a mold to restore perfectly the external form of the organism or skeleton. Perhaps, because of the relatively high cost of the acids in former days, this method of preparing fossils never was extensively exploited until about thirty years ago. G. Arthur Cooper has developed refined methods of preparing fossils at the U. S. National Museum by means of dilute acids. Many kinds of plants, invertebrates, and vertebrates are being successfully prepared in this way. In certain limestones and dolomites many of the calcareous fossils have been selectively replaced by silica without appreciable modifications of the calcareous matrix. The soluble rock matrix may be carefully dissolved away from the fossils with suitable acids. This method combines the advantages of mass collecting with chemical preparation and fossils preserved in this way as siliceous pseudomorphs are almost certainly more abundant than generally supposed. From thirty to forty tons of Permian limestone collected in the Glass Mountains of Texas, Cooper has extracted an estimated three million invertebrate fossils, the majority of which are exquisitely preserved. The morphology of a large proportion of the species now can be worked out for the first time. A control block of limestone weighing one hundred and eighty-six pounds yielded ten thousand excellent specimens of invertebrates, including Foraminifera, brachiopods, bryozoans, gastropods, and pelecypods. Only a very few of these fossils were exposed on the surface of the rock and none could have been completely cleaned of matrix by mechanical means. Whole new faunas of mid-Ordovician trilobites preserved in the same way have been worked out by Whittington and Evitt (1954) and others.

One of the greatest obstacles in the study of fossil vertebrate remains has been the tedious and difficult extraction of the bones from hard rock matrix. The principal substance of vertebrate bones, conodonts, and certain brachiopods, is calcium phosphate

which is nearly insoluble in acetic and formic acids. These acids can, therefore, be used to dissolve limestone from phosphatic fossils. Many delicate and complex structures have been cleaned perfectly of hard matrix by this means. Usually the matrix contains much insoluble material so that the chemical preparation must be supplemented by manual cleaning under a microscope.

SUMMARY

These illustrations, I believe, demonstrate that the limitations of the fossil record are not so much a matter of poor preservation or insufficient quantity but rather insufficient collecting and inefficient methods of preparing fossils. New discoveries of fossils and rapid improvements in techniques have greatly expanded the possibilities for a far more complete knowledge of past life than we now possess. The future prospects for paleontology are, indeed, very bright if an ample supply of dedicated and expert paleontologists can be trained and oriented toward systematic exploration of the fossil record.

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